

THE GILLS OF CHITONS (POLYPLACOPHORA) AND THEIR SIGNIFICANCE IN MOLLUSCAN PHYLOGENY

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ABSTRACT

It was demonstrated in 1965 that gills of chitons are not paired structures but are added during growth and can show asymmetry. More recent studies, largely on living *Chaetopleura apiculata* (Say) at Woods Hole, confirm the broad homologies of each chiton gill with the aspidobranch ctenidium retained in several stocks of Archaeogastropoda. In particular, similar organization is found of afferent and efferent blood vessels in the gill axis; of alternating ctenidial leaflets; and of lateral, frontal, and abfrontal cilia. In addition to like ciliary functions, both the gastropod aspidobranch gill and each individual chiton gill show similar neuromuscular reflexes in cleansing mucus-bound sediment. One difference, due to the functional organization of each row of chiton gills into a pallial curtain dividing the mantle groove, is the occurrence of Velcro-like ciliary junctions. Unlike junctions in mytilid and other "filibranch" bivalves, which are modified lateral cilia linking adjacent filaments on the same gill, these ciliary junctions link leaflets on adjacent gills and probably represent modified frontal cilia. The coordinated and dynamic functioning of this ctenidial curtain is emphasized, and it is suggested that the adaptive basis on which chitons evolved a curtain by replicating gills, rather than by elongation of ctenidial parts, results from the dynamic pallial groove (unlike the fixed shapes of pallial cavities in bivalves and shelled gastropods). Otherwise chiton gills, along with those of protobranchiate bivalves and certain archaeogastropods, are little altered from "archetypic" molluscan ctenidia.

All archetypes are speculative, available as temporary models of ancestors to be tested by predictions and retrodictions. However, data on gills and other replicated structures in chitons (like data on *Neopilina*, and on molluscan capacity for degrowth) appear to exclude hypotheses involving true metameric segmentation from models of ancestral molluscs.

The multiplied organ systems found in chitons have to be considered in any discussion of metamerism in primitive molluscs. It was demonstrated several years ago (Russell Hunter and Brown, 1965) that the gills of chitons are not paired structures but are added singly during growth, with the result that several species show asymmetry in ctenidial numbers between the left and right sides of individual chitons. Gills continued to be added in adults to meet increased respiratory needs with growth of live tissue mass, and it was concluded that the rows of ctenidia, and probably the other multiplied structures in chitons, reflect functional replication (Russell Hunter and Brown, 1965) rather than the vestiges of more extensive ancestral segmentation as assumed by Lemche (1959b, 1966). The significant feature of the gill rows in dividing the mantle grooves of chitons into functionally inhalant and exhalant chambers had been elucidated by Yonge (1939), and

this also stressed functional rather than vestigial multiplication of the gills. Since the discovery in 1952 of the living monoplacophoran genus, *Neopilina* (Lemche, 1957; Lemche and Wingstrand, 1959), discussion of possible metamerism in primitive molluscs has been revised, and continues into the 1980's. Recent Russian investigators of the multiplied structures of chitons (Minichev and Sirenko, 1984) have again concluded that there is no evidence of annelid-like metamerism in their morphogenesis. In his most recent, and beautifully detailed, account of anatomy in Monoplacophora, Wingstrand (1985) still concludes that in chitons, "an oligomeric repetition, probably 7- or 8-metamerism is present" (p. 87, see also pp. 77-81). Given the currency of such divergent views, it seemed appropriate to use this symposium on the Biology of Polyplacophora to present some more recent observations on the functioning of the gills in living chitons. These studies

were mostly carried out with *Chaetopleura apiculata* (Say) at Woods Hole.

The material presented here involves not only the functional morphology of individual ctenidia in living chitons, but also their combined dynamics as a gill curtain. Two general aspects will be emphasized. First, each chiton gill is a true ctenidium, structurally and functionally homologous with the aspidobranch gill in certain archaeogastropods and with the more primitive gills of protobranchiate bivalves. In addition to reviewing the integrated ciliary and circulatory functions, new observations are presented on neuromuscular cleansing reflexes common to all these primitive molluscan ctenidia. Secondly, new observations give emphasis to the coordinated functioning of the replicated gills as a ctenidial curtain dividing the inhalant from the exhalant pallial chambers, but conforming dynamically to the changing shape and hydraulics of each pallial groove. Some speculation on this as the likely adaptive basis for gill replication in chitons follows, along with a discussion of these and other multiplied structures of chitons. Finally, the implications of such functional replication are considered in relation to hypotheses on interrelationships among the major classes of molluscs, and on metameric segmentation in models of ancestral molluscs.

MATERIALS AND METHODS

In 1979-80 and again in 1986-87, living specimens of *Chaetopleura apiculata* (Say) were studied at the Marine Biological Laboratory (MBL), Woods Hole. This is the "Common Eastern Chiton" of the Atlantic seaboard of the northeastern United States, and most of the material came from boulders on the Buzzards Bay side of Penzance Point near Woods Hole. Other early observations on gills in living specimens of *Lepidochitona cinerea* (L.) were carried out in 1961-63 in Scotland. Over the years 1961-87, other casual observations on living chitons have been made on *Tonicella marmorea* (Fabricius) and *Acanthochitona crinita* (Pennant) in Scotland, and on *T. rubra* (L.) in Massachusetts and Maine. The only observations on *Lepidopleurus cancellatus* (Sowerby) and *L. asellus* (Gmelin) were on material already fixed.

Most observations were made under dissecting microscope (at magnifications from X7 to X30) using incident lighting, with living chitons crawling inverted under glass slides, or on the convex sides of watch glasses. A few observations utilized a temporary "inverted microscope" arrangement of a dissecting microscope pod to check on water currents in chitons crawling dorsal side up (that is with pallial grooves and their contained ctenidia directed downwards). Elucidation of water and ciliary currents, and mapping of mucous secretion and accumulation, involved the injection of particles into the pallial grooves. Particles used included fine carborundum, carmine, Ankolor scarlet S, and dried milk powder. The three figures are diagrams, admittedly reductionist cartoons, each derived from sets of many sketches. Figure 1 is basically from *Lepidochitona*, and figures 2 and 3 from *Chaetopleura*. Some specimens were preserved after partial narcotization using propylene phenoxetol (for details of this method, see Russell Hunter and Brown, 1965), fixa-

tion in 12% formalin in sea water, and storage in 10% glycerol. Temporary microscope mounts were made of individual gills, both living and fixed, for viewing both by incident and by transmitted light.

OBSERVATIONS

GENERAL ARRANGEMENT AND NUMERICAL ASYMMETRY

In chitons, the mantle cavity is in the form of two narrow pallial grooves running between the foot and the broad mantle edge or girdle on each side. Each pallial groove contains a row of gills, the bases of which are attached deep in the groove on the girdle side (Fig. 1). The gill curtain forms a functional division of the pallial groove longitudinally into an inhalant chamber, ventral on the girdle side, and an exhalant chamber placed dorsally and pedally (Fig. 1B). As in all molluscan mantle complexes, the anus along with kidney and genital openings discharge in the exhalant stream. Newly formed ctenidia are at the anterior end of each row (Fig. 1A). As growth continues in adult chitons, ctenidia are added anteriorly, irregularly and independently on each side. However, for any species of chiton, there is always a broad correlation between gill number and adult tissue mass (Russell Hunter and Brown, 1965). Asymmetry in ctenidial numbers between the left and right sides of individual chitons occurs in most chiton species. For populations of four chiton species studied in detail, the percentages of asymmetric individuals were 19.5%, 46.3%, 48.4% and 69% (Russell Hunter and Brown, 1965). In most species the numbers of individual chitons with extra left gills are apparently balanced by the numbers with extra right gills. However, Gowlett-Holmes and Zeidler (1987) have described a new species, *Acanthochitona saundersi*, for which all available specimens have 11 ctenidia on the right side and 10 ctenidia on the left side. Asymmetries of ctenidial numbers have been found in at least fifteen species of chitons, and could well occur in the majority of chiton species (Minichev and Sirenko, 1984; A. M. Jones, pers. comm.).

CTENIDIAL FUNCTIONAL MORPHOLOGY

When the gills of a living chiton are viewed from the ventral side, the free tips are seen to be directed toward the edge of the foot (the inner wall of the pallial groove). The gills bulge convexly toward the observer and their axes are defined by the prominent efferent branchial vessels (Fig. 2, ebv). The other (exhalant) face of each axis contains the narrower afferent branchial vessel. The leaflets, which alternate on either side of the gill axis, are short and wide (almost semicircular in face view, Fig. 3), and their tips are opposed (one to one, or one to two) to the tips of leaflets on the next ctenidium in the row (Fig. 2).

Water is moved dorsally (and pedally) by broad bands of lateral cilia (which are more flagella-like) toward the inner and posteriorly directed exhalant chamber (Fig. 3), in a physiologically efficient counter-flow to the blood circulation (afferent branchial vessel to efferent branchial vessel) within

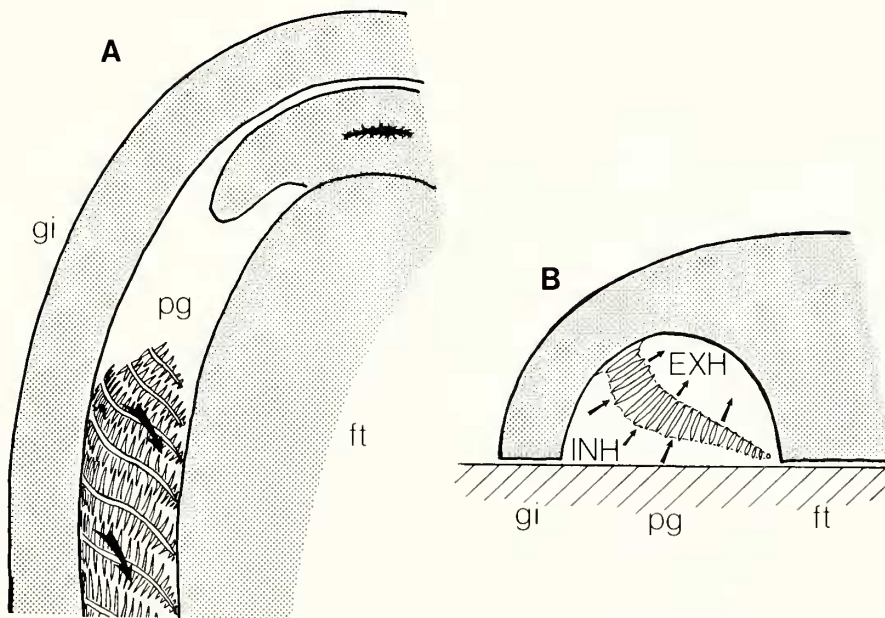


Fig. 1. Diagrams of the mantle groove in a chiton (based on *Lepidochitona*) showing (A) ventral aspect of anterior part of groove, and (B) cross-section of the groove at a central ctenidium. Note that inhalant part of the groove (INH) is girdle-ventral and exhalant part (EXH) is pedal-dorsal (gi, girdle; ft, foot; pg, pallial groove).

each ctenidial leaflet. On the inhalant (INH) side the edges of the leaflets bear shorter frontal cilia (that is, on the facing edges of Fig. 2), and on the exhalant (EXH) side the leaflet edges bear abfrontal cilia. Both frontal and abfrontal cilia have a cleansing (particle-moving) function rather than water propulsion, and transport particles around the leaflet edges toward the axis. The free tips of each leaflet bear specialized longer, less motile cilia that entangle in a Velcro-like fastening (x on Fig. 3) with the corresponding cilia on the leaflet tips of the adjacent ctenidium. From their position, and development in ctenidial buds, these ciliary junctions linking adjacent gills probably represent modified frontal cilia.

The assemblage of microstructures and their functions shown by the chiton gill are thus essentially similar to those found in the primitive "aspidobranch" plume gill of the Archaeogastropoda. If an individual chiton gill is specifically compared with the single plume gill in the limpet, *Acmaea testudinalis* (Müller), the only significant difference involves the Velcro-like ciliary junctions on the chiton leaflet tips. There are obviously minor differences of microanatomy such as the outline proportions of the leaflets, and the distribution of lateral cilia on the leaflet faces, but these seem trivial in comparison with the broader concert of structures and functions. The gill axes with alternating leaflets are essentially identical in arrangement, as are the dorsal afferent branchial vessel and the ventral efferent vessel carrying oxygenated blood back to the heart. The lateral, frontal and abfrontal cilia are arranged in the same way and, in both, the lateral cilia produce a flow of water through the gill (and through the mantle cavity) in the opposite direction to the blood flow. Chiton gills are true ctenidia, structurally and functionally homologous with those of other molluscs. The rows of chiton gills are clearly not neomorphic structures, secondary respiratory organs as in

some marine limpets like *Patella*, or in various groups of freshwater pulmonate snails (Russell-Hunter, 1978; McMahon, 1983), but have to be regarded as rows of multiplied ctenidia.

CTENIDIAL CLEANSING REFLEX

Surprisingly little attention has been paid to the muscular movements of primitive molluscan ctenidia. A relatively new set of observations on chiton gills concerns the fact that each ctenidium can move in a patterned cleansing reflex. To anticipate a little, the sequence of movements in the individual chiton ctenidium seems to be exactly similar to that in the cleansing "flick" of the single plume gill in forms like *Acmaea*.

In the axis of the chiton ctenidium, longitudinal muscle fibers lie around and below the two major blood vessels. When both sets of muscle strands contract together, the gill is shortened and pulled toward its base, with a consequent decrease in the gill's contained blood volume. Gill retraction of this sort can be accomplished in 0.2 to 0.8 seconds. Re-extension of the gill is always slower (several seconds) with blood being passed in hydraulically by action of distant antagonists. If the muscle under the afferent branchial vessel alone contracts (stretching the muscle on the efferent side) then the gill curls up into the pallial groove, the ctenidial tip moving away from the foot (Figs. 1, 2). In the opposite case, if the muscle under the efferent branchial vessel contracts the whole gill is straightened and its tip could hit the foot edge or the substratum-surface or both.

If the cleansing cilia (frontal) are experimentally loaded by introducing material (suitably dense but small, like fine grade carborundum) onto the inhalant face of the gill, the foreign particles become mucous-bound and are moved

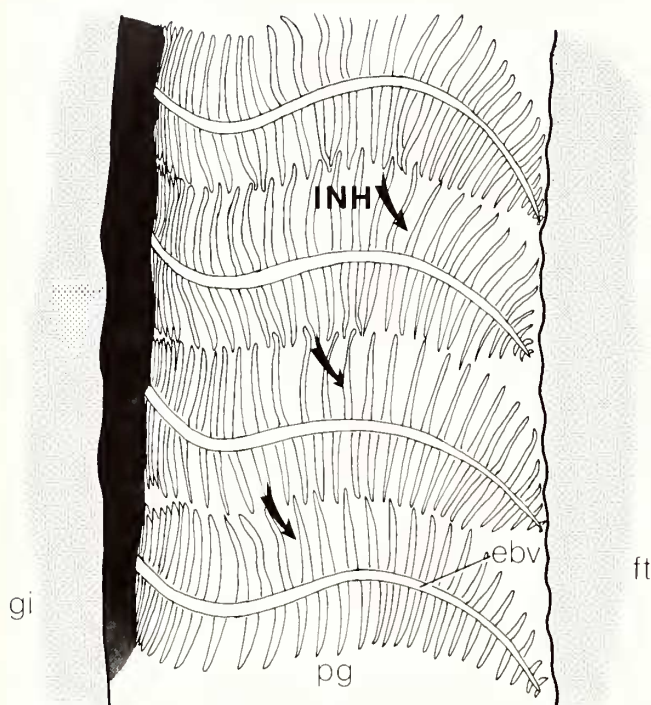


Fig. 2. Diagrammatic view of four ctenidia in *Chaetopleura* from the ventral inhalant side (INH). The axes show the efferent branchial vessels (ebv), and there are frontal cilia on the facing edges of the leaflets. Note that the tips of leaflets are opposed one to one, or one to two (INH, inhalant current; gi, girdle; ft, foot; pg, pallial groove).

toward the axial ciliary tract (Fig. 3) and thence toward the gill tip. In a healthy chiton, accumulation of this sort at the tip provokes a reflex action sequence. The reflex is not gravity dependent and can be observed in chitons in all postural relations to the horizontal. The same reflex takes place if foreign material is loaded on the abfrontal (exhalant) face of the gill. The patterned cleansing reflex occurs in three sequential phases. First, for two to three seconds, more blood is pushed in while the gill expands. (It is difficult to measure this, but the overall volume increase at this phase is usually between 20% and 50%). Secondly, the muscle strands under the afferent branchial vessel contract relatively slowly, taking between 2 and 5 seconds. Thirdly, the muscle under the efferent branchial vessel contracts relatively rapidly, taking between 0.1 and 0.2 seconds, and flicks the tip toward the foot and substratum-surface while simultaneously shortening the gill. (Only at this stage is the contained blood volume reduced again.) In most cases a mucous-bound pellet of natural sediment, or foreign particles, leaves the gill surface and remains on the cilia of the pedal edge or on the substratum. It should be noted that there is never any question of ciliary junctions being formed (even temporarily) between the gill tip cilia and the pedal cilia.

Despite the subtle differences in ctenidial proportions noted above, this reflex action of the individual chiton gill (acting, it seems, in a neuromuscular sense as a peripheral reflex, or almost as an independent effector system) involves a patterned sequence exactly following that observed in the

aspidobranch gill of *Acmaea*. Parenthetically, it is worth noting one somewhat special case observed in living chitons, concerning the last large gill in *Chaetopleura*. On several occasions it has been observed to "flick" material right out of the pallial groove, with its tip passing under the girdle in a temporary (and asymmetric) lifting more like the usual local arching of the girdle for typical temporary inhalant openings. Of course, this can only occur because of the distinctly different siting of that last large gill, with its tip directed posteriorly and girdlewards instead of toward the midline and foot. In this respect as others, conditions in the lepidopleurid chitons must be quite different, but we lack observations of living gill movements. In typically near-holobranch chitons like *Chaetopleura* and *Lepidochitona*, groups of three or more ctenidia can flick together. This leads to the second group of new observations.

THE COORDINATED CTENIDIAL CURTAIN

Even the casual observer of the underside of a living chiton can see (Fig. 2) the functional organization of each row of chiton gills into a pallial curtain dividing the mantle groove along most of its length into inhalant and exhalant chambers. This is functionally dependent upon the occurrence of Velcro-like ciliary fastenings on the leaflet tips of chiton gills. Unlike the ciliary junctions in mytilid and other "filibranch" bivalves which are modified lateral cilia linking adjacent filaments on the same ctenidium, these ciliary junctions in chitons link leaflets on adjacent gills and probably represent modified frontal cilia. If the filibranch gills typical of mussels, scallops or oysters are disturbed mechanically, the ctenidial filaments become tangled and the coordinated filtering and sorting functions are temporarily lost. Given otherwise healthy conditions and a little time (usually only a few minutes), the filaments will "crawl" by ciliary action over each other until the appropriate ciliary junctions are reconnected and the seemingly continuous corrugated lamella re-established as a porous water-propelling and filtering surface. Similar processes occur if the ctenidial curtain is mechanically disturbed in a healthy chiton. Individual gills can carry out slower flicks across the pallial groove, but the main re-establishment of the curtain involves the ctenidial tips being "walked" (largely by ciliary action) along the side and edge of the foot, and over each other until an orderly row is again set up. With re-establishment of the row, the ciliary junctions reconnect the tip of one posterior leaflet either to one or to two anterior leaflets on the gill behind it.

In healthy chitons, the way in which each ctenidial row moves as a single dynamic curtain is impressive. It bulges and flattens to accommodate changes in the hydraulics of the pallial groove resulting from shifts in the inhalant (and less frequently the exhalant) openings across the girdle as the chiton crawls along. The early observation of Yonge (1939) that inhalant openings can be formed by local lifting of the girdle at almost any point along the anterior part of the chiton is clearly confirmed. Yonge's conjecture, that the capacity for creating inhalant openings back along the sides of the body is valuable when the anterior end is out of the water, can be supported by the observation that, in *Chaetopleura* at least,

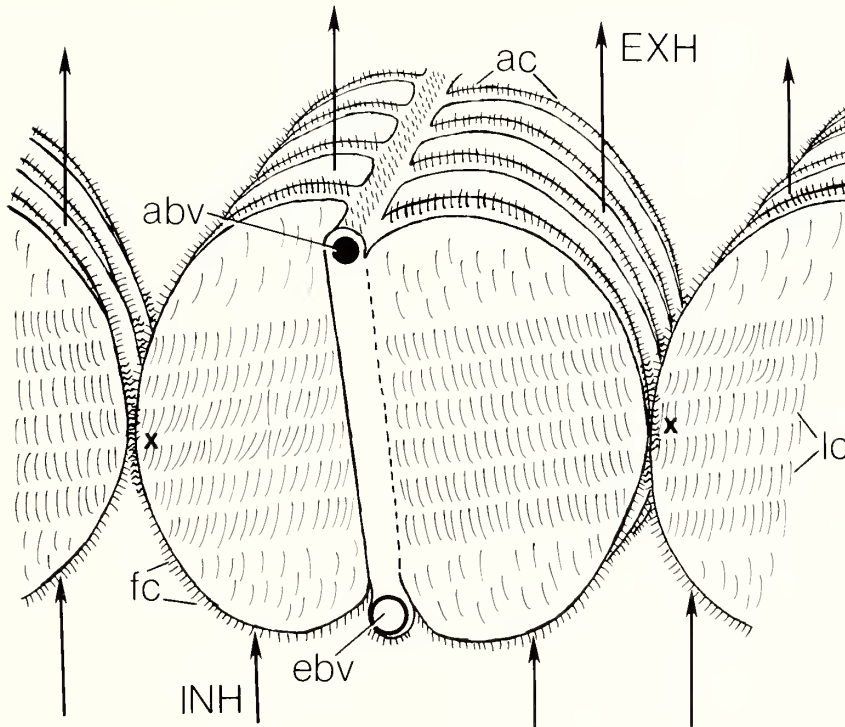


Fig. 3. Stereogram of part of a chiton ctenidium. Water is moved dorsally (and pedally) by bands of lateral cilia (lc). On the inhalant (INH) side, the ctenidial leaflet edges bear front cilia (fc) and the ctenidial axis contains the efferent branchial vessel (ebv). On the exhalant (EXH) side, the leaflet edges bear abfrontal cilia (ac) and the gill axis contains afferent branchial vessel (abv). The opposed free tips of the leaflets bear specialized cilia forming the Velcro-like ciliary junctions (x), probably representing modified frontal cilia.

the continuity of the ctenidial curtain is maintained even with air-bubbles in the anterior third of the groove on both inhalant and exhalant sides of the gill row. Yonge (1939) also noted that the exhalant opening across the girdle was less variable in position, being always at the posterior end. At first sight this seems true in living *Chaetopleura*, and the anus in the midline is always swept by a strong exhalant current. However, while the arching of the girdle to form an exhalant opening always occurs close to the anus, its size (with water velocity inversely related) and its direction (to left or to right of the midline) do vary. As such changes occur, accommodation of the ctenidial curtain to pressure shifts involves it becoming less convex (more flattened towards the foot, decreasing the exhalant cavity volume) or more convex (decreasing the inhalant fraction of the pallial cavity). Changes resulting from shifts in size or direction of the exhalant opening can be particularly obvious in a chiton crawling over a curved or irregular surface. Once again, the simplest set-up used to view a chiton through a flat glass surface can be deceptive.

Working with both living specimens and models of mopalid chitons, R. S. Cox and his colleagues have applied water flow visualization techniques in flow tanks and have noted muscular contractions of the pallial groove walls (Douglas J. Eernisse, pers. comm.). They have had only equivocal evidence of pallial shape producing augmentation of flow (such as ramming or Bernoulli effects), but my observations suggest that the chiton's ability to modify the exhalant

(downstream) pressure by changes in the effective diameter of its exhalant girdle opening could have some significance in shifting the fluid dynamics of the pallial system. Despite this, basic water propulsion and consequent differential pressures in the pallial compartments must all result from the activity of the lateral cilia on the ctenidial leaflets. It is noteworthy that, even in adult chitons, there are always some bands of ciliated epithelia on the walls of the pallial groove which beat in a posterior direction (particularly on the inside of the girdle). Such ciliation is obvious in young (30-day) postlarval chitons, where it exists before the first ctenidial buds and creates analogous water currents (Russell Hunter and Brown, 1965). However, in adults these cilia seem to propel superficial strings of mucus rather than the ambient water.

Despite the adjustments of walls and openings, the dynamic continuity of the ctenidial curtain is maintained as the living chiton crawls along. The direction of the gill axes, with their obvious efferent branchial vessels (Fig. 2), can be seen to be altered but adjacent axes always stay more or less parallel. Groups of six to eight (or occasionally more) gills move together, with their gill-tips lagging behind the foot as the chiton crawls forward, or making a fast recovery so that the gill-tips are seen to be moving forward relative to the edge of the foot. Similarly, groups of ctenidia acting together can move their tips toward and away from the pedal edge. This must involve neural coordination in, for example, the simultaneous contraction of the afferent muscle strands in

eight adjacent gills. Some part of the continuity of the curtain could be passive after the ciliary junctions have been connected, but there are obviously also active movements involving the coordination of several ctenidia or even most of the ctenidial row. The ctenidial curtain sometimes shows a metachronal wave of forward movement independent of the foot, or a group of tips crawling together along the foot. Again the loose or temporary attachment of ctenidial tips to the pedal edge does not include any Velcro-like action, although mucous-bound packages of cleansed material are often passed to the foot. In addition, it was already noted that groups of three or more gills could be simultaneously involved in the faster cleansing reflex.

ADAPTIVE SIGNIFICANCE OF THE GILL CURTAIN

Perhaps the most important observation to be made about the whole mantle groove system in chitons is that it is dynamic. Unlike the pallial cavity of a bivalve or shelled gastropod with its relatively static dimensions and shape, the chiton pallial groove is a chamber bounded by pedal and girdle walls whose shapes continually change with movements of the chiton. The chamber wall provided by the habitat surface (Fig. 1B) can also change markedly, since chitons can and do crawl round corners and over edges. Thus the ctenidial curtain has to conform (as a continuous, water-pumping, porous partition) not only to the inhalant and exhalant imposed pressure changes noted above but also to the shape changes of the whole groove system. This is probably the reason why chitons have evolved their pallial curtain by replication of a series of gills rather than by the elongation of axes or of filaments (leaflets) in one pair (or two pairs) of ctenidia. Leaving aside consideration of the evolution of the higher lamellibranch bivalves, the potential for hypertrophy of single units of molluscan ctenidia is amply demonstrated in certain gastropods. In Calyptraeid prosobranchs, a water-propulsive ctenidial curtain is achieved by the elongation into filaments of the leaflets of a single pectinibranch (one-sided) gill. It is proposed that an adaptive functional explanation for the evolution of ctenidial replication in chitons is provided by the dynamic nature of the mantle grooves in the group.

Admittedly, there are two obvious omissions in this survey of the functioning of the ctenidial curtain in chitons. First, there are almost no comparative data on gill function in chitons with Lepidopleurid and other patterns of posterior gills. Although many (perhaps most) species of chitons have long gill rows essentially like those in *Chaetopleura*, *Lepidochitona* and *Tonicella*, a variety of other conditions have been described. Early workers, such as Pelseneer (1897), developed a syntagma, or array of holobranch and mero-branch forms, with metamacrobranchs and mesomacrobranchs, and with or without adanales. A simpler, and probably more functionally significant, classification of certain gill position characters has been utilized by D. J. Eernisse (pers. comm.) in the course of revising the probable higher-level phylogenetic relationships among chitons. Even the most skeptical approach to the use of pallial cavity structures in chiton classification has to separate the Lepidopleurids. Again it would be helpful to know something of comparative gill func-

tion in these forms, as well as something of comparative development (Minichev and Sirenko, 1984).

Recent studies on variation in larger population samples of common European chitons (A. M. Jones, pers. comm.) have emphasized the need for a population approach to assessing taxonomic characters. Even in *Chaetopleura*, usually described as holobranch, two distinct forms occur within the populations studied at Woods Hole (Russell Hunter and Brown, 1965) differing in the extent to which each pallial groove is occupied by the ctenidial row. In one form the bases of the gills extend forward for only about 75% of the pallial groove, while in the other the bases extend anteriorly as far as the head fold, and thus conform to the accepted species diagnosis. It is possible that these could reflect phenotypic growth responses to levels of microhabitat oxygenation, but D. J. Eernisse (pers. comm.) has pointed out that, given the lack of knowledge of these stocks, subsequent investigation of other character states might well establish the two forms as separate subspecies or even species. However, none of the new observations presented in this paper would be invalidated if it were subsequently proven that the studied specimens of *Chaetopleura apiculata* from near Woods Hole belonged in two distinct but congeneric species.

The second gap in this presentation on the functioning of the ctenidial curtain in chitons involves the lack of any studies on the ultrastructure of the cilia concerned (particularly those of the ciliary junctions). Any interested investigator with access to SEM facilities, and appropriate techniques of narcotization and fixation, could elucidate much of interest.

SUMMARY OF OBSERVATIONS

Even with these two major omissions, the observations on gills in living chitons can be summarized as five topics. First, the gills are not paired structures but can be added asymmetrically during continued adult growth. Secondly, each gill appears to be structurally and functionally homologous with the aspidobranch ctenidium of archaeogastropods. Thirdly, a neuromuscular cleansing reflex is common to the gills of both chitons and archaeogastropods. Fourthly, each of the two gill rows in chitons is organized as a coordinated ctenidial curtain utilizing ciliary junctions. Fifthly, the adaptive significance of ctenidial replication in chitons (rather than hypertrophy of single units) could lie in the dynamic nature of the pallial space.

DISCUSSION

Many aspects of the phylogeny of molluscs, and of molluscan ancestry, remain controversial. The observations presented here on the gills of living chitons have significance only in relation to two of these aspects: first, the structural and functional homologies of ctenidia and, secondly, the possible metamerism of ancestral molluscs. They can contribute little or nothing to other debates in molluscan phylogeny, such as whether the primitive mantle-cavity was a pallial groove surrounding the head-foot or a posterior cavity with a complex of paired pallial structures, or if the primitive

mantle was dome-shaped and secreted a one-piece shell. Similarly, questions of the relationships between the three major classes of "modern" molluscs and the Aplacophora, Monoplacophora and Polyplacophora are barely glossed by this work. The two pertinent questions of ctenidial homologies and of ancestral metamerism both merit further discussion, but the former can be dealt with more simply and its near enthymeme is set out first. Ancestral metamerism requires both some conceptual history and more extensive and multilateral exposition, and these will follow.

In evolutionary hypotheses, organ structures are considered homologous in two or more animal forms if they can be claimed as being derived from a common precursor organ structure in a common ancestral animal (Mayr, 1969, 1983; Russell-Hunter, 1979). Such theoretical claims are normally based on similarity of fundamental structural plan in the organs concerned, on similar anatomical associations with other organs, and on similarities in their embryonic development. Since such claims are inferential, most modern evolutionists would prefer them to be phrased in terms of maximum likelihood. When, as in the case of the molluscan pallial cavity and ctenidium, we have a whole concert of organs and functions operating in an integrated fashion, there is likely to exist what can be termed functional homology (Russell-Hunter, 1968, 1979). It can be deduced that extensive patterns of functional interdependence must be encoded by largish packets of integrated genetic material commonly derived (since the precursor animal must also have been an efficient machine with similar functional interdependence). Cytogenetic levels of linkage need not be postulated. On the other hand, attempts at the enumeration of discrete unit characters for the molluscan ctenidium and its associated pallial complex for either cladistic (Hennig, 1950, 1966) or phenetic analysis would be relatively uninformative from such an integrated system (Mayr, 1974, 1983). The ctenidium, a gill with characteristic patterns of ciliated epithelia and blood vessels, is found as a homologous structure in Gastropoda, Bivalvia, and Cephalopoda (Yonge, 1947).

In each mollusc with them, the ctenidia are part of an integrated functional system: the heart and other blood vessels, certain glands and sense-organs, the external openings of genital and renal systems, and the posterior part of the alimentary canal are all structurally and functionally stereotyped in their relationships to the ctenidia. As pointed out elsewhere (Russell-Hunter, 1968, 1979), it is highly significant that, although probably at least 75,000 molluscan species (out of about 110,000) have ctenidia, and although there are many aquatic animals belonging to other phyla which seemingly could make good use of a ctenidium, no nonmolluscan animal has one. The above observations on gills in living chitons can only confirm the conclusion reached by Yonge (1939, 1947) that the gill rows represent multiplied ctenidia. David R. Lindberg (pers. comm.) remains unconvinced of homology between gills of chitons and those of gastropods, largely on the basis of differences between the two classes in the blood vessels draining the haemocoelic spaces of the body and supplying the afferent branchial vessels of the gills. However, it is not the preafferent circulation that links the

ctenidium with its associated pericardial and pallial structures in a functionally homologous complex, but the postefferent connections to the auricles, auriculoventricular openings, and the rest that do so. Further, there is considerable variation within gastropods in the arrangement of the preafferent vessels. The attempt by Lemche (see especially Lemche, 1966) to suggest that bivalves and cephalopods have gills of different origin from those of gastropods was based on a misunderstanding of the relationships of their suspensory ligaments in respect to the branchial vessels. It was associated with his claims for homology between the gills of chitons and those of *Neopilina* (Lemche, 1959a, 1966) and, in turn, between the gills of *Neopilina* and the limbs of arthropods like trilobites (Lemche, 1959b, 1966). Each chiton gill is a true ctenidium, structurally and functionally homologous with the aspidobranch gills of Archaeogastropoda and the protobranch gills of more primitive Bivalvia. Again, it has to be admitted that this concluding hypothesis of homology for chiton gills makes little contribution to the vexed questions of further homology with the gills of *Neopilina* (Lemche, 1966) or with the gills in certain Aplacophora (Scheltema, 1973, 1988).

The other phylogenetic controversy, that on metameric segmentation in the ancestral mollusc, is less easy to set forth. Before attempting to outline its history and arguments, some statement of premises regarding both metameric segmentation and archetypes as models of ancestors may be appropriate. The essence of metameric segmentation as found in annelids and arthropods is the serial succession of segments each containing unit-subdivisions of the several organ systems (Hyman 1951; Russell-Hunter, 1968, 1979). The sequence of morphogenesis of these segments is antero-posterior from a penultimate budding zone, so that the segments just behind the head are older, and the more posterior ones (just in front of the budding zone) are younger. The differentiation of additional segments in this mode of morphogenesis is such that each new segment contains (at least initially or potentially) a full set of all organ systems.

Archetypes are not ancestors. For any stock of animals, the characteristics of the actual ancestral forms will never be known with certainty. Archetypes are logical constructs, temporary models set up from reductionist explanations of available data, to be tested by the collection of further data. The testing can invalidate, but can never authenticate (despite the current belief of certain systematists that their cladistic hypotheses can be confirmed by separately computed phenetic analyses). When considering such models, in view of what Mayr (1983) terms "cohesion of the genotype", it seems particularly important to consider possible functional homologies as well as the more usual morphological ones (Russell-Hunter, 1979). Significant functional unity is apparent within each phylum of more complex animals (including molluscs, arthropods, echinoderms, and chordates). There are obvious pragmatic values in setting up ancestral models. There are peculiar dangers in evolutionary discussions after setting up an archetype, and these seem to result from assembling together in the unfortunate hypothetical animal a group of incompatible structures, all thought to be "primitive" or "plesiomorphic" within the stock. As noted

elsewhere (Russell-Hunter, 1968, 1979), many of these dangers can be avoided if, when a hypothetical ancestral type is constructed, an attempt is made to create a working archetype — one in which the concert of organs and functions could operate as a whole, in an integrated functional plan, as in all living organisms. In discussing similar matters in the adaptive morphology of vertebrates, Bock (1965) (see also Bock and von Wahlert, 1965) has clearly stated the need for analyses of function in the whole animal. The working archetype (Russell-Hunter, 1968, 1979) can be set up from a deduced concert of structures and functions together forming an integrated functional plan, and can then provide a better basis for phylogenetic speculation and both predictive and retrodictive testing.

Molluscan archetypes with short segmented bodies had been proposed by Pelseneer (1899, 1906) and Naef (1926), largely on the basis of studies on the genital and excretory systems of chitons and cephalopods. However, the extensive and convincing work of the molluscan functional morphologists such as Yonge, Graham and Fretter on ciliary mechanisms, ctenidial blood vessels, and renopericardial and genital ducts (particularly in more primitive gastropods) set up a very different model for the stem-mollusc. As set out in fecund summary by Yonge (1947), although primitively bilaterally symmetrical, this archetype was totally unsegmented and possessed a posterior mantle-cavity enclosing a pallial complex of paired structures which included two ctenidia. This model convincingly survived retrodictive testing against the fossil record, as clearly set out by Knight (1952) who was able to fit appropriate pallial circulation and muscle attachments into the lower palaeozoic monoplacophoran genera, *Scenella* and *Pilina*, regarded then as untorted "pregastropods." Pragmatically, it is important to note that versions of Yonge's model are still employed in the 1980's by systematists (Salvini-Plawen, 1980; Seed, 1983) and pedagogues (Russell-Hunter, 1979, 1982) both as gastropod archetype and as bivalve archetype and, as regards the paired pallial structures and homologous ctenidia of these two stocks, have survived much testing.

Discussion of possible metamerism in ancestral molluscs was reopened by the discovery of a living monoplacophoran, *Neopilina*, by its preliminary description (Lemche, 1957) and by the extensive description of its morphology (Lemche and Wingstrand, 1959) that followed. It was hypothesized that the mollusc ancestor must have shown relatively complete metamerism, that this is present to a somewhat reduced extent in *Neopilina*, that this is still further reduced in chitons, and that this metamerism degenerates so completely as to be undetectable in gastropods and bivalves (Lemche and Wingstrand, 1959). Subsequently Lemche (1966) reversed part of this hypothesis and claimed that the arthropods originated directly from a molluscan ancestor. For a few years, many strange phylogenies were based on *Neopilina* as a "missing link" rather than as an interesting survivor of a less successful molluscan stock. In this respect, the claims of homology among the gills of chitons, the gills of *Neopilina*, and the arthropod limbs of trilobites (Lemche 1959b, 1966) begin to approach the idealist metabiological comparisons

of William Patten. As noted elsewhere (Russell-Hunter, 1985), Patten's use, early in this century of detailed comparative anatomy to postulate an origin of vertebrates in arachnids (or merostomatids like *Limulus*), represents a comparatively late derivative of the *Naturphilosophen* of Johann Wolfgang von Goethe (1749-1832), and is perhaps closest in concept to the publications of Lorenz Oken in the first half of the nineteenth century. Even without idealist morphology, in the work of Lemche and Wingstrand (1959) on *Neopilina*, and in the beautiful reconstructions subsequently presented by Wingstrand (1985), it is explicit that the multiplied organs of chitons (shells-valves, muscles, gills and nerves) reflect metameric segmentation. Indeed, after detailed comparisons of *Neopilina*, *Vema* and chitons, Wingstrand (1985) concludes that a homologous 8-metamerism is present in the Polyplacophora. Such a chiton archetype with true metamerism can be tested appropriately with the data on actual replicated structures in chitons including the numbers and symmetry of gills (Russell Hunter and Brown, 1965), and the functioning of the gill series (this paper). Even when the other multiplied structures are considered, there is little of the serial succession of segments, each with unit subdivisions of organ systems, in any living chiton, and there is no evidence of serial organogenesis. The mantle rudiment of a settled postlarval chiton secretes six plates. After an interval a larger anterior plate is added then, still later, a small posterior plate. There is never a budding zone as in the annelid-arthropod mode of development. Segmentation in heart structures is even less valid. Chitons all have an elongate ventricle in the midline which receives blood from two symmetrical elongate auricles. Most chitons have two pairs of auriculoventricular openings, several genera have one pair, and chiton species are known with three pairs and with four pairs. Both *Neopilina* and *Nautilus* have four auricles and therefore also have two pairs of auriculoventricular openings. Individual ctenidia in chitons cannot be related to any other replicated organs, such as shell-valves, nephridial lobes, lateropodal nerve connections or heart structures, and thus cannot be allocated to specific metameric segments. Other features of chiton gills and their functioning complete this negation of the metameric archetype for chitons. The gills are not paired but are added asymmetrically during continued adult growth. As individual gills, they seem to be structurally and functionally homologous with those of primitive bivalves. This replication in chitons results in gill rows, which show coordinated function as pallial curtains and cannot reflect simplification of more extensive metamerism. Ctenidial replication in chitons can be claimed to result adaptively from the dynamic nature of the pallial grooves in the chiton body form.

Similar arguments can be used to criticize the concept of annelid-arthropod metamerism applied to the described structures of *Neopilina* and *Vema*. This statement should not be taken as critical of the majority of the interesting homologies elucidated by Wingstrand (1985), in particular his meticulously exhibited parallels between chitons and the two monoplacophoran genera not only in pedal retractor muscles but also in the muscles of the buccal mass and radula. However, living monoplacophorans have five (or six) pairs of

gills, eight pairs of pedal retractor muscles, two pairs of auricles, six (or seven) pairs of nephridiopores, two (or three) pairs of gonads, and a single shell (Wingstrand, 1985). This assemblage is unlikely to have arisen by segmental morphogenesis.

In his claims for molluscan metamerism, Wingstrand (1985) appears to rely on the concept of a monophyletic Protostomia or Spiralia, linked by common features of early cleavage, gut development and larval type. It may be best to quote his own words (Wingstrand, 1985: 89): "The metamerism of molluscs is in itself hardly unexpected, for many features support their incorporation within the Spiralia, a group in which different kinds of metameric repetition are common." Unfortunately, the concept of a group of phyla forming the Spiralia is itself suspect. The five diagnostic features used to discriminate the group from the Deuterostomia are neither so universal nor so consistent as to justify a clear dichotomy (Russell-Hunter, 1979). Larval homologies have been in doubt since Garstang (1922, 1929) seriously challenged recapitulation as an important factor in the evolution of larval stages. Cleavage is a dynamic process in time and spiral cleavage is not absolutely correlated with mosaic development. As Costello (1948, 1955) pointed out, there are three main categories of cleavage (radial, bilateral and spiral), and three basic types of spiral cleavage (by quartets, by duets and by monets), but all are modified into bilateral cleavage later in development. He emphasized that the occurrence of spiral cleavage has no obvious significance in the interrelationships of animal phyla (Costello and Henley, 1976).

There is another kind of developmental evidence linking molluscs and flatworms and making molluscan metamerism less likely. Recent work on actuarial bioenergetics has emphasized the capacity for degrowth in some shelled molluscs (Russell-Hunter *et al.*, 1983, 1984; Russell-Hunter, 1985), and compared it in flatworms. Along with other features of indeterminate growth, many gastropods and bivalves show a capacity to degrow (as individuals to reduce the mass of their structural proteins under certain circumstances), no close-coupling of growth with sexual maturation, and a lack of endogenous senescence (Russell-Hunter and Eversole, 1976; Russell-Hunter and Buckley, 1983; Russell-Hunter, 1985). It has been hypothesized (Russell-Hunter, 1985) that this capacity in flatworms and molluscs could involve controls of genetic expression that cannot coexist with those involved in a metameric pattern of morphogenesis. Some molecular biologists studying ageing indicate accumulated errors in the synthesis of macromolecules as important (Kirkwood, 1977; Kirkwood and Holliday, 1979), and they correlate the absence of endogenous senescence in certain organisms with indeterminate growth patterns. The neuro-hormonal and hormonal controls for metameric development may mandate selective gene-expression in some irrevocable fashion that is incompatible with cellular dedifferentiation-rejuvenation, and with the capacity of degrowth exhibited by molluscs and flatworms. This hypothesis of incongruent controls of morphogenesis in molluscs and in metamERICALLY segmented animals cannot yet be tested experimentally. That it can be proposed illustrates the weight of circumstantial

evidence that metameric organogenesis of the sort which produces serial sets of structures in the phyla Annelida and Arthropoda never occurs in the Mollusca.

As already admitted, conditions in the stem-mollusc remain controversial. The general conclusion from the present work that chitons do not show true metameric segmentation seems established at a high level of likelihood. Extending the logic, evidences against metamerism of the annelid-arthropod pattern in all primitive molluscs are strong, and a consensus with the views of Wingstrand and of Salvini-Plawen could be achieved if their protoannelid ancestor for the molluscan stock were totally without metameric segmentation, indeed if it were an unsegmented flatworm turned coelomate. All model ancestors are highly speculative.

At the end of the earlier paper on chiton gills (Russell-Hunter and Brown, 1965), an archetype mollusc with a four-fold basic organization (that is, with four ctenidia, four auricles, four renal organs, etc.) was proposed. This derived from a footnote query by C. F. A. Pantin in Yonge (1947), and reflected the heart morphology of *Neopilina*, *Nautilus* and chitons. Somewhat surprisingly, this model is mentioned favorably not only by Minichev and Sirenko (1984) but also in passing by Wingstrand (1985). From such a four-fold organization, two sorts of subsequent morphogenesis could occur. Both a line of organisms with one gill on either side, and a line with many, could thus evolve from an archetype with two pairs of gills. In this hypothesis, the former stock (that is, those with one pair of ctenidia, one pair of auricles, one pair of renal organs, and so on) could still be regarded as archetypic for the two major groups of living molluscs: the gastropods and the bivalves. But, as reiterated pedantically here and elsewhere, archetypes are not ancestors.

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